R EXD.

Vol. 91. Part 6. Pp. 145–173, 28 figs. 17th November, 1941

IMP. INST. ENT.
LIBRARY
18 NOV 1941
RIAL Eu. 344
PARATE

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGE

Cowley, J., M.A. A new species of *Protoneura* from Peru, and a review of the group of *Protoneura tenuis* Selys (Odonata, Protoneuridae) 145–173, 28 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 6s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1941–1942.

K. G. Blair, D.Sc., *President.*

Prof. P. A. Buxton, M.A.
G. Fox-Wilson, N.D.H.
Hugh Main, B.Sc. } *Vice-Presidents.*

Brigadier W. H. Evans, C.S.I., C.I.E., D.S.O., *Treasurer.*

N. D. Riley, *Secretary.*

F. J. Griffin, A.L.A., *Registrar.*

Other Members of Council.

Prof. H. G. Champion, C.I.E., M.A.
E. A. Cockayne, M.A., M.D., F.R.C.P.
A. S. Corbet, D.Sc., Ph.D., F.I.C.
Col. F. A. Labouchere.
A. M. Massee, D.Sc.
C. Potter, B.Sc., Ph.D.
O. W. Richards, M.A., D.Sc.
The Hon. Miriam Rothschild.
J. Smart, B.Sc., Ph.D.
W. H. T. Tams.
A. Welti.

Finance and House Committee.

A. Welti (Chairman).

H. M. Edelsten.
A. G. Gabriel.
C. N. Hawkins.
Francis Hemming, C.M.G., C.B.E.
J. Smart, B.Sc., Ph.D.

Publication Committee.

O. W. Richards, M.A., D.Sc. (Chairman).

E. A. Cockayne, M.A., M.D., F.R.C.P.
G. Fox-Wilson.
A. M. Massee, D.Sc.
W. H. T. Tams.
V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S.

Library Committee.

Prof. P. A. Buxton, M.A. (Chairman).

E. B. Britton.
A. S. Corbet, D.Sc., Ph.D., F.I.C.
B. M. Hobby, M.A., D.Phil.
F. Laing.
R. W. Lloyd.

Committee for the Protection of British Insects.

W. G. Sheldon (Chairman).

Capt. E. Bagwell-Purefoy.
C. L. Collenette.
W. J. Dow.
J. C. F. Fryer, O.B.E., M.A.
Col. F. A. Labouchere.
N. D. Riley.
H. M. Edelsten (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Sir Guy A. K. Marshall, C.M.G., D.Sc., F.R.S., appointed 1939.
   Dr. Karl Jordan, F.R.S., appointed 1936.
2. **International Congress of Entomology** (Berlin 1938).
   J. C. F. Fryer, O.B.E., M.A. *Francis Hemming, C.M.G., C.B.E.*
   A. D. Imms, M.A., Sc.D., F.R.S.
3. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten. *Mr. E. C. Bedwell.*
   [Delegates nominated by Committee for the Protection of British Insects.]
4. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. W. G. Sheldon, appointed 1922.
5. **New Forest Association.**
   Mr. W. Fassnidge, appointed 1934.
6. **Royal Meteorological Society. Phenological Committee.**
   Dr. C. B. Williams, appointed 1937.

A NEW SPECIES OF *PROTONEURA* FROM PERU, AND A REVIEW OF THE GROUP OF *PROTONEURA TENUIS* SELYS (ODONATA, PROTONEURIDAE)

By J. Cowley, M.A.

Manuscript received 10th July, 1940.

Read 6th November, 1940.

With Twenty-eight Text-figures.

Contents.

	PAGE
Introduction and description of *Protoneura klugi* sp. n.	145
Definitions of measurements	158
Discussion of ratios	161
Corrections and additions to previous descriptions	162
The *tenuis* group of *Protoneura*	164
Historical	164
Relationships of the species	165
Discussion of the characters of the genus *Protoneura* and of the *tenuis* group	167
Taxonomic value of the postnodal and postsubnodal series of cross-veins	169
Revised definition of *Protoneura* Selys, 1857	169
Definition of *tenuis* group	170
Key to the species of the *tenuis* group of *Protoneura*	171
References	173

Introduction.

In connection with her studies of species of *Protoneura* (Cowley and Gloyd, 1938; Gloyd, 1939) I forwarded to Mrs. Leonora K. Gloyd a single female of a *Protoneura* from Iquitos, Peru. Mrs. Gloyd believed it to represent a new species, but in the absence of associated males refrained from describing it. Since her studies were completed I have received from the same locality a single male *Protoneura* from the collector Mr. Guillermo G. Klug, and I therefore now describe it, and have pleasure in naming it after Mr. Klug (following here as seems appropriate the example set by the names of two recently described species of the same group), from whom I have received much interesting material. I wish to thank Mrs. Gloyd for her assistance in the study of the female and for general aid in the study of this group.

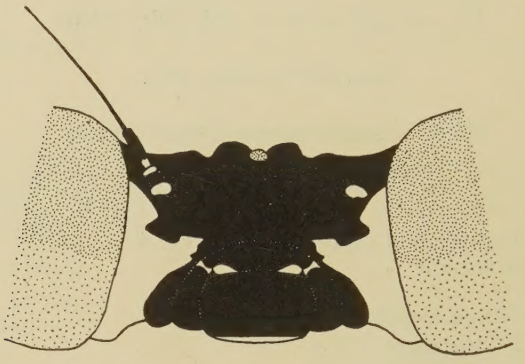
Protoneura klugi sp. n.

Male Holotype.

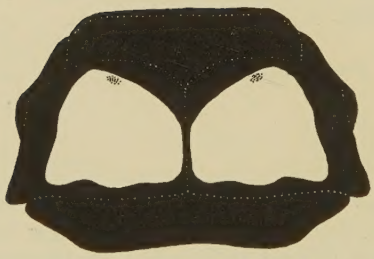
Head (fig. 1). Labium cream coloured, median lobe cleft to 0·46 of its length; labrum glossy black, narrowly bordered anteriorly with yellow; mandibles with the bases laterally glossy black, mesal portion covered by the labrum cream; anteclypeus glossy black, at the anterior margin a small yellow spot at the external angle, occupying about one-third of the margin; postclypeus glossy black; frons black, below each antenna a glossy area reaching to the postclypeus, with two yellow spots across the anterior face placed laterally

at the base of each antenna and about equal in size to the median ocellus; vertex black; dorsal surface of head entirely black except for a very small, scarcely visible, triangular yellow-brown area at the margin of the eye on a level with the lateral ocellus; genae mostly yellow; antennae black with the external surface and apical ring of scape and basal third of pedicel yellow; rear of head entirely black; eyes dark brown above, yellow-brown below, the two colours clearly separated, not intergrading.

Prothorax (figs. 2–3). Anterior lobe black; median lobe black with two large dorsal



1



2

3

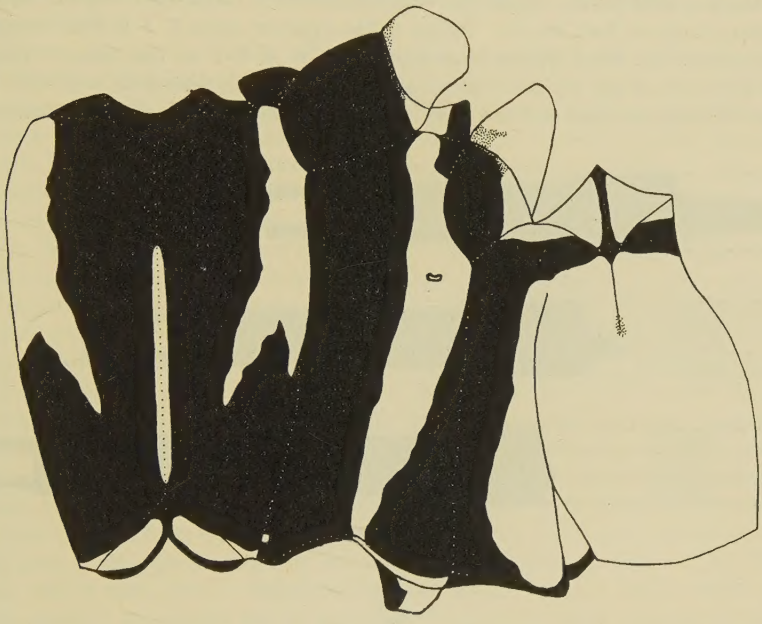
All figures drawn with the camera lucida, except those described as diagrammatic.

FIGS. 1–3.—*Protoneura klugi* sp. n., holotype ♂. 1, anterior view of head, diagrammatic; 2–3, dorsal and right lateral views of prothorax.

scarlet-orange spots narrowly separated by a median black line, occupying the greater part of the dorsum; close to the anterior margin each bears a minute obscure blackish spot; pleura entirely black; posterior lobe black, the posterior margin convex but almost straight mesally in normal view,[1] similar to *P. tenuis* (Cowley and Gloyd, 1938 : pl. II fig. 4); prosternum black.

[1] I use the term " normal view " to denote a view perpendicular (normal) to a surface or structure; in the case of somewhat curved surfaces, this would be taken as being perpendicular to the " mean plane " of the surface. In fig. 2 the posterior margin of the posterior lobe appears to be less largely convex and the mesal portion even concave, because the lobe is not viewed normally.

Pterothorax (fig. 4). Black with pale areas as follows: a narrow scarlet-orange stripe, about 0·1 mm. wide, on the apical $\frac{1}{10}$ of the mid-dorsal carina; a scarlet-orange antehumeral stripe touching the basal half of the mesopleural (humeral) suture below, forked apically somewhat before half the length of the mesepisternum, the mesal branch tapering apically and extending slightly mesad and caudad, reaching to $\frac{2}{3}$ of the length of the mesepisternum, lateral branch tapered apically, much shorter, scarcely leaving the mesopleural suture, asymmetrical, being shorter on the left side, the maximum width of the stripe basal to the fork about 0·23 mm. or $\frac{1}{20}$ of the width of the mesepisternum; antealar sinus largely scarlet-orange mesally, shading to yellow laterally; a small yellow spot in the apico-dorsal corner of the mesepimeron; a yellow area in the apico-ventral corners



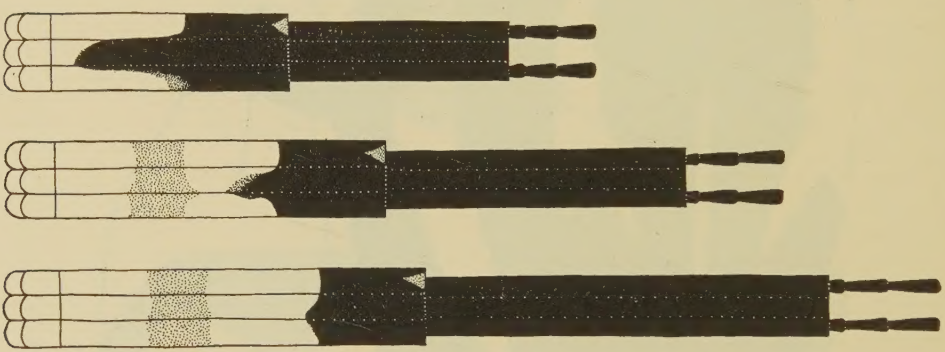
4

FIG. 4.—*Protoneura klugi* sp. n., holotype ♂. Colour-pattern of pterothorax, diagrammatic, showing the dorsum, right side and venter.

of the mes- and metinfraepisterna; a yellow stripe on the metepisternum in juxtaposition with the interpleural (first lateral) suture above, reaching the basal margin of the sclerite, tapered apically, narrowed basal to the metaspiracle; lateral part of metepimeron with a yellow area ventrad, apically more than half the width of the sclerite, tapered basally to less than half the width, not reaching the basal margin of the metepimeron, the width of the black band over the metapleural (second lateral) suture at mid-length about equal to the maximum width of the metepisternal pale stripe; basal margin of metepimeron with a small yellow area continuous with the pale area of the metinfraepisternum; mesosternum with the anterior half yellow and continuous with the pale areas of the mesinfraepisternum and metepisternum; metasternum largely pale yellow, continuous with the pale ventral area of the metepimeron, only narrowly black mid-ventrally; the part of the metepimeron on the venter pale yellow, the black band of the lateral part continued ventrally to meet its fellow from the other side and the metasternal mid-ventral black;

poststernum pale yellow; meso- and metaterga dark brown to black with small pale yellow spots.

Legs (fig. 5). Coxae pale yellow with a brown basal spot anteriorly, largest on the first pair, smallest on the second pair; trochanters pale yellow; femora, first pair with the anterodorsal surface black except for a basal pale yellow area $\frac{1}{11}$ of its length, posterodorsal surface with an apical black area extending diagonally from the base of the black area on the anterodorsal surface to the base of the black area on the ventral surface, which area occupies a little less than the apical half, second and third pair black apically with the basal $\frac{2}{3}$ (basal $\frac{3}{8}$ on the anterodorsal surface) and $\frac{13}{20}$, respectively, pale yellow divided by a broad grey band at about half the length of the pale area; tibiae and tarsi entirely black or dark brown; tarsal claws dark amber with black tips; femoral, tibial and tarsal spines black or dark brown. Spines of the anterior series 3, 5–6, 6 in number on the first, second and third femora respectively, 3 + 8, 5, 6–7 on the tibiae [2]; posterior series 3, 6–7, 8–9 on the femora [3]; distal anterior spine 1·22, 0·75–0·82, 0·53–0·67 times the length between its base and the base of the preceding spine on the first, second and



5

Fig. 5.—*Protoneura klugi* sp. n., holotype ♂. Colour-pattern of first, second and third pairs of legs, diagrammatic, showing the ventral, anterodorsal and posterodorsal surfaces of each.

third femora respectively, proximal anterior spine 0·83, 0·58–0·65, 0·53–0·65 times the length between its base and the base of the succeeding spine on the tibiae.

Wings. Hyaline, venation black or dark brown, pterostigma brown, over slightly less than one cell in front wings, one cell or slightly less in hind-wings; postnodals, 10 front wings, 9 hind-wings; postsubnodals, 10 front wings, 8 hind-wings; superior sector of triangle (Cu_2) crossing the subnodal transversal (which reaches the posterior margin of the wing) and reaching the posterior wing-margin $\frac{1}{4}$ or $\frac{1}{3}$ of a cell beyond; median

[2] The figures 3 + 8 for the first tibiae indicate 3 spines proximal to the first modified spine of the tibial comb, spines of the tibial comb together with spines distal thereto (which are difficult to distinguish accurately from the tibial comb, but in the species studied here there appear to be 1–2, perhaps in one case 3, unmodified distal spines) 8 in number; modified basal spines of the femoral comb scarcely visible or perhaps absent in the species studied.

[3] Posterior series of spines on the tibiae not studied, as in papered specimens of which the legs are often close together the distal spines are particularly difficult to count with any accuracy.

sector (R_{4+5}) arises about half a cell before the subnodus; subnodal sector (IR_3) arises at the subnodus; median (R_{4+5}) and subnodal (IR_3) sectors at the subnodus just distinct (joined in one hind-wing); nodal sector (R_3) arises front wings at 5th, hind-wings at 4th postsubnodal (and postnodal); postnodal sector (IR_2) arises front wings at 9th postsubnodal (and postnodal), hind-wings at 8th postsubnodal (at 8th or $\frac{1}{3}$ of a cell beyond 8th postnodal); first antenodal costal space distinctly the longest, second about $\frac{3}{4}$ the length of third, second and third together subequal to first (one front wing, one hind-wing) or $\frac{1}{6}$ (one front wing), $\frac{1}{10}$ (one hind-wing) longer than first; width of wings slightly more than $\frac{1}{8}$, front wings, slightly less than $\frac{1}{7}$, hind-wings, of the length; distance from base of wing to nodus just over $\frac{1}{3}$ of the wing-length and equalling the distance from the nodus to or nearly to the 6th (front wings), to just beyond the 6th (hind-wings) postnodal.

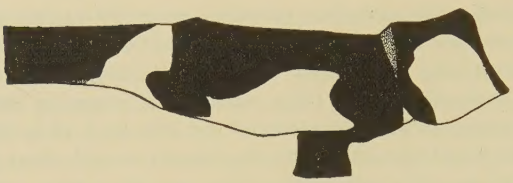
Abdomen (figs. 6, 7, 10, 12). Black dorsally; segment 1 pale yellow laterally, the dorsal black continued along the apical margin; segment 2 black with a large lateral pale yellow area extending to the ventral margin, in the basal and apical quarters of the segment the dorsal black extends laterally to the ventral margin; anterior genital lamina black; segments 3–6 laterally brown blending with the dorsal and apical black, 3 with a narrow basal yellowish ring, almost divided mid-dorsally, broadened laterally and confluent with the lateral pale colour, 4–6 with a narrow basal bluish-green ring obscurely divided mid-dorsally, laterally merging to brownish-yellow and confluent with the lateral brown, so that 4–6 appear to bear a pair of small basal pale spots; segment 7 with a pair of small greenish-yellow basal spots, entirely separated mid-dorsally, not confluent laterally with a narrow ventral border of deep yellow which extends the entire length of the segment, a little broadened basally and apically; segment 8 black with a broad ventral border of yellow, expanded subapically; segment 9 black with the entire ventral border very narrowly yellow, a small yellow spot at the baso-ventral angle narrowly separated from the ventral border, a large yellow subapical lateral spot confluent with the pale ventral border, enlarged basad below mid-height of the segment, then tapered and nearly meeting its fellow of the other side mid-dorsally; segment 10 entirely black, the apical margin with a rounded excision from whose edge there slopes down a shelf which continues the more lateral part of the apical margin of the segment. Sternites: segment 1 and base of 2 yellow; vesicle dark brown; segments 3–7 dark brown; 8 black, dusky yellow apically; 9 black basal to the genital valves, dusky yellow apical to them, the valves black with dusky yellow apical and mesal borders; 10 entirely black. Apical carinae of segments 7–9 only distinctly denticulate.

Penis (figs. 8–9). Terminal segment with lateral lobes at mid-length small, apically the lateral margin produced as a process directed dorsad, not sclerotised, the apex of the process expanded, truncated, apical margin between the processes slightly concave; shaft spines absent.

Abdominal Appendages (figs. 10–13). Superiors very slightly shorter than abdominal segment 10, subequal to the inferiors; broad at the base with the mesal subbasal tubercle not very distinct and with a conspicuous dorso-lateral depression; mesal margin almost straight; tapered to a rounded inwardly curved apex; in lateral view, the apex decurved and bearing a minute subapical ventral tooth; ventral lamina large, light brown, arising at about the middle of the ventral surface of the appendage, curved dorsad, the apex subacute and directed caudad; coloration black mesally, brown laterally and ventrally. Inferiors broad at base, then subcylindrical and only slightly curved laterally; coloration, lower half of base black, the rest brown, the middle portion of the narrowed part darker, the extreme apex paler.

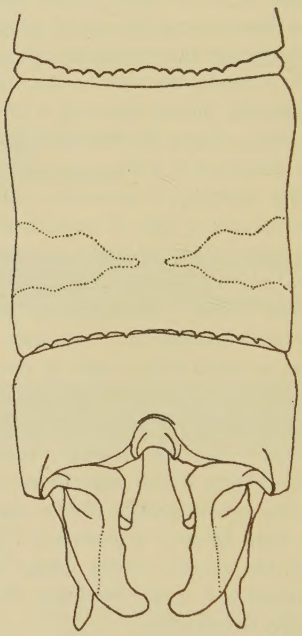
Measurements [4] (in mm.). Maximum breadth of head and eyes (He), 2·95; maximum

[4] The definitions of these measurements are given below, p. 158.



6

8



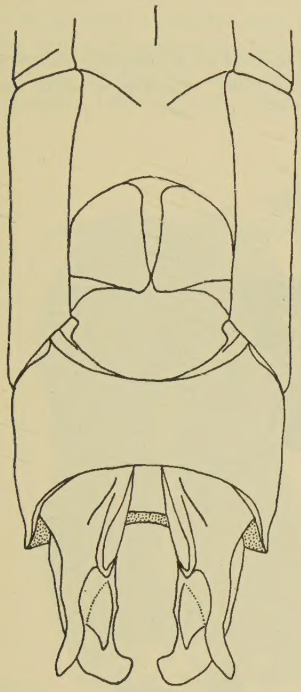
10

9

7

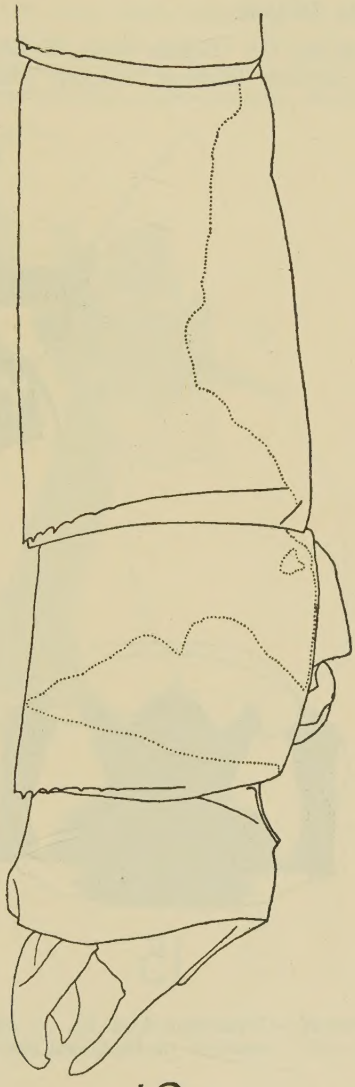
FIGS. 6–10.—*Protoneura klugi* sp. n., holotype ♂. 6, right lateral view of abdominal segments 1, 2 and part of 3; 7, colour-pattern of abdomen, diagrammatic, dorsal aspect on the left, lateral aspect on the right; 8–9, dorsal and left lateral views of penis; 10, dorsal and ventral views of abdominal segments 9–10 and appendages.

breadth of occiput (Ho), 2·05; maximum length of head (Hl), 1·35; length of mesepisternum (M), 2·38; lateral width of pterothorax (P), 1·91; length of first tibia (T_1) 1·91, of third (T_3) 2·33; length of front wing (Wl_1) 19, of hind-wing (Wl_2) 17·5; maximum



11

13



12

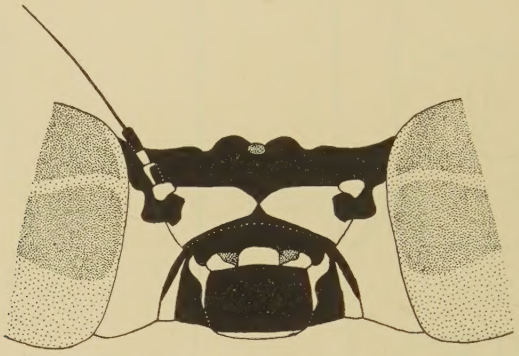
FIGS. 11–13.—*Protoneura klugi* sp. n., holotype ♂. 11, dorsal and ventral views of abdominal segments 9–10 and appendages ; 12, right lateral view of abdominal segments 8–10 and appendages; 13, supero-internal view of left superior appendage.

width of front wing (Wb_1) 2·47, of hind-wing (Wb_2) 2·45; costal length of pterostigma, front wing 0·53–0·56, hind-wing 0·56; maximum width of pterostigma front and hind-wing, 0·37; length of abdomen plus appendages, 32·5; length of abdominal appendages, superior 0·40, inferior 0·49.

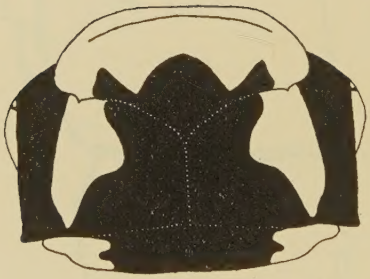
Ratios.[5] He/Ho 1·443, Hl/Ho 0·659, Ho/M 0·863, Hl/M 0·569, P/M 0·804, T_3/T_1 1·220, T_3/M 0·980, Wb_1/Wl_1 0·130, Wb_2/Wl_2 0·140, length/width pterostigma, front wing 1·438–1·500, hind-wing 1·500, Wl_2/M 7·351, A/Wl_2 1·857, A/M 13·66.

Female Allotype.

Head (fig. 14). Labium cream, median lobe cleft to 0·44 of its length; labrum glossy black, narrowly bordered anteriorly with brownish-yellow; mandibles with the bases



14



15

16

FIGS. 14–16.—*Protoneura klugi* sp. n., allotype ♀. 14, anterior view of head, diagrammatic; 15–16, dorsal and right lateral views of prothorax.

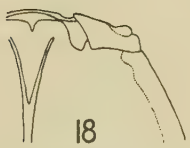
laterally glossy black, the upper margin cream; anteclypeus glossy, cream with a brown triangle, the apex of which just reaches the apical margin, at each side of the middle of the basal margin; postclypeus glossy black; frons largely cream, narrowly black mid-dorsally and with a black spot, a little larger than the median ocellus, about its own width below the base of each antenna; vertex black; dorsal surface of head entirely black, no triangular pale area at the margin of the eye; genae largely cream; antennae black with the external surface and apical ring of the scape and rather more than the basal third

[5] A discussion of these ratios is given below, p. 161.

of the pedicel cream; rear of head entirely black; eyes brownish-yellow, above with two well-marked darker brown areas.

Prothorax (figs. 15–16). Anterior lobe cream, a basal black spot which is rounded mesally and extends to about half the length of the lobe, again extending apicad, but not so far, laterally; median lobe black with two cream stripes extending the length of the lobe, the mid-dorsal black separating them equal to the greatest width of a stripe; pleura black, the ventral angle cream and immediately anterior thereto a minute cream spot; posterior lobe with about the mesal two quarters black, yellow laterally, the posterior

17



18

FIGS. 17–18.—*Protoneura klugi* sp. n., allotype ♀. 17, colour-pattern of pterothorax, diagrammatic, showing the dorsum, right side and venter; 18, dorsal view of right mesostigmal lamina.

margin convex, in normal view[6] a little flattened mesally, somewhat sinuous laterally, similar to *P. tenuis* (Cowley and Gloyd, 1938 : pl. III fig. 5); prosternum black.

Pterothorax (figs. 17–18). Black with pale (cream) areas as follows: a narrow stripe (about 0·1 mm. wide) on the apical $\frac{2}{3}$ of the mid-dorsal carina; an antehumeral stripe along rather more than the basal half of the mesopleural (humeral) suture, its width at mid-length about 0·14 mm. or $\frac{3}{14}$ of the width of the mesepisternum; antealar sinus with a U-shaped marking, the open end of the U apico-lateral; a small spot in the apico-dorsal corner of

[6] See footnote 1, p. 146.

the mesepimeron; a small area in the apico-ventral corners of the mes- and metinfraepisterna; a stripe on the metepisternum in juxtaposition with the interpleural (first lateral) suture above, reaching the basal margin of the sclerite, tapered apically, narrowed basal to the metaspiracle and then again widened; lateral part of the metepimeron pale ventrad, apically the pale area more than half the width of the sclerite, tapered basally to less than half the width, reaching the basal margin of the metepimeron and continuous with the pale colour of the metinfraepisternum, the width of the black band over the metapleural (second lateral) suture at mid-length slightly less than the maximum width of the metepisternal pale stripe; mesosternum with the anterior half pale and continuous with the pale areas of the mesinfraepisternum and metepisternum; metasternum largely pale, continuous with the pale area of the metepimeron, black mid-ventrally; the part of the metepimeron on venter pale, its basal margin with a narrow dark brown stripe extending from the metasternal mid-ventral black to the ventral margin of the lateral part of the sclerite, widely separated from the black of the lateral part of the sclerite; poststernum cream; meso- and metaterga dark brown to black with small cream spots. Mesostigmal lamina (fig. 18) simple, triangular, on a slightly higher plane than the mesepisterna, black, the anterior margin with a low rounded cream-coloured elevation.

Legs (fig. 19). Coxae cream with a small brown basal spot anteriorly, scarcely indicated on the first pair; colour-pattern of the rest of the legs as in the male, except that the basal pale areas occupy about the basal $\frac{1}{2}$, $\frac{2}{3}$ and $\frac{2}{3}$ of the anterodorsal surface of the first, second and third femora respectively, on the first femora the apical black scarcely longer on the anterodorsal than on the ventral surface, and thus more nearly resembling the pattern of the second and third femora than does that of the first femora in the male. Spines of the anterior series 3, 6, 6 in number on the first, second and third femora respectively, 3 + 9, 6, 7–8 on the tibiae [7]; posterior series 3, 7, 8–9 on the femora [8]; distal anterior spine 0·90, 0·89, 0·80–0·83 times the length between its base and the base of the preceding spine on the first, second and third femora respectively, proximal anterior spine 1·11, 0·83, 0·73–0·79 times the length between its base and the base of the succeeding spine on the tibiae.

Wings. Hyaline, venation black or dark brown, pterostigma brown, over slightly less than one cell in all wings; postnodals 9–10 front wings, 8 hind-wings; postsubnodals 9 front wings, 7–8 hind-wings; superior sector of the triangle (Cu_2) in the left front wing and both hind-wings crossing the subnodal transversal (which reaches the posterior wing-margin), reaching the posterior wing-margin $\frac{1}{4}$ of a cell beyond, in the right front wing the subnodal transversal does not reach the posterior wing-margin but ends on the superior sector of the triangle (Cu_2) which reaches the posterior wing-margin $\frac{1}{8}$ of a cell beyond (or, superior sector of the triangle ending against the subnodal transversal); median sector (R_{4+5}) arises about half a cell before the subnodus; subnodal sector (IR_3) arises at the subnodus; median (R_{4+5}) and subnodal (IR_3) sectors at the subnodus distinctly separated; nodal sector (R_3) arises front wings at 4th, or $\frac{3}{4}$ of a cell distal to 4th, hind-wings at 4th postsubnodal (and postnodal); postnodal sector (IR_2) arises front wings at 8th, hind-wings at 7th postsubnodal (and postnodal) or $\frac{2}{3}$ of a cell distal to 7th postsubnodal ($\frac{1}{3}$ of a cell distal to 8th postnodal); first antenodal costal space distinctly the longest, second about $\frac{2}{3}$ (one front wing and hind-wings) or $\frac{5}{8}$ (one front wing) length of third, second and third together $\frac{1}{5}$ longer than first in all wings; width of all wings slightly more than $\frac{1}{7}$ of the length: distance from base of wing to nodus just under (front wings) or just over (hind-wings) $\frac{1}{3}$ of the wing-length and equalling the distance from nodus to $\frac{1}{4}$ of a cell beyond the 5th (front wings) or more than $\frac{1}{3}$ of a cell beyond the 5th (hind-wings) postnodal.

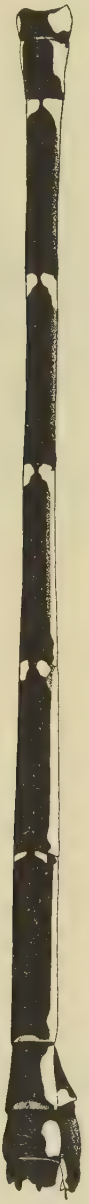
Abdomen (figs. 20–23). Black dorsally; segment 1 cream laterally, the dorsal black

[7] See footnote 2, p. 148.

[8] See footnote 3, p. 148.

19

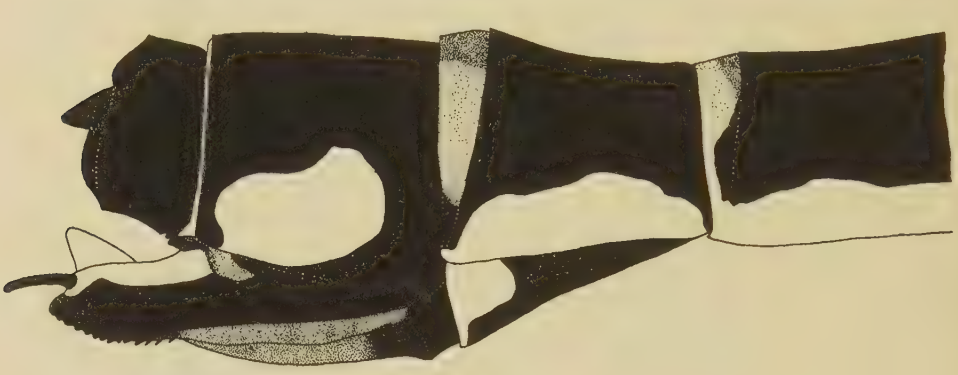
20



21

FIGS. 19–21.—*Protoneura klugi* sp. n., allotype ♀. 19, colour-pattern of first trochanter and femur (only base of the black tibiae shown), diagrammatic, showing the ventral, anterodorsal and posterodorsal surfaces; 20, right lateral view of abdominal segments 1, 2 and part of 3; 21, colour-pattern of abdomen, diagrammatic, dorsal aspect on the left, lateral aspect on the right.

continued along the apical margin; segment 2 black with a large lateral cream area, about half the height of the segment at mid-length, narrowed apically and not reaching the apical margin; segments 3–7 cream or yellow laterally along the ventral margin, extending the whole length of the segments, very narrow on 3 and 4, broadening on 5, fairly broad on 6 and 7, above changing through brown to the dorsal black, basally confluent with the pale dorsal spots on 3–5, separated therefrom on 6 and 7; 3–7 with a basal greenish-yellow ring interrupted mid-dorsally, narrowly so on 3, more broadly divided



22

23

Figs. 22–23.—*Protoneura klugi* sp. n., allotype ♀. 22, right lateral view of abdominal segments 7 (apex only) and 8–10 and appendages; 23, teeth on outer valve of ovipositor, left lateral view.

on each succeeding segment, the two dorsal spots thus formed largest on 3, diminishing in size to 7 where they are narrow and widely separated, on 3–5 broadened laterally and confluent with the lateral pale colour; segments 8–9 entirely black dorsally, the apical rings of 7–9 (broad on 7 and 8, narrow on 9) pale brown above, darker laterally, segment 8 with a yellow latero-ventral area extending the whole length of the segment, about $\frac{1}{3}$ the height of the segment at mid-length, 9 with a lateral yellow spot which only reaches the ventral margin posteriorly, and which extends about half-way to the dorsum; segment 10 entirely black; superior appendages black, periprocts black, their mesal margins narrowly brownish-yellow. Sternites: 1 cream, 2 cream with a broad transverse band before the

middle, 3–7 brown, darker on each succeeding segment, black on 6 and 7, the apical margin of 7 narrowly yellow-brown, 8 black with an apico-lateral yellow spot which is continued along the apical margin as a narrow border to meet its fellow. Ovipositor reaching to the level of the apex of the superior appendages; basal plate black, inner valves black at the base, apical part largely brown, outer valves black, the ventral border against the inner valves narrowly brown, the free apical dorsal border rather broadly yellow, the apical ventral border with 14 large broad teeth preceded by 4 small ones [9] (fig. 23); styles black. Apical carinae of segments 7–9 only distinctly denticulate.

Measurements [10] (in mm.). Maximum width of head and eyes (He) 2·84, maximum width of occiput (Ho) 1·98, maximum length of head (Hl) 1·42, length of mesepisternum (M) 2·33, lateral width of pterothorax (P) 1·88, length of first tibia (T_1) 1·95, of third (T_3) 2·38, length of front wing (Wl_1) 19, of hind-wing (Wl_2) 18, maximum width of front wing (Wb_1) 2·77, of hind-wing (Wb_2) 2·72, costal length of pterostigma front wing 0·56, hind-wing 0·56–0·62, maximum width of pterostigma front and hind-wings 0·37, length of abdomen plus appendages 27, length of superior abdominal appendages 0·19, length of ovipositor (excluding style) 1·53.

Ratios.[11] He/Ho 1·435, Hl/Ho 0·718, Ho/M 0·850, Hl/M 0·610, P/M 0·810, T_3/T_1 1·215, T_3/M 1·020, Wb_1/Wl_1 0·146, Wb_2/Wl_2 0·151, length/width pterostigma, front wing 1·514, hind-wing 1·514–1·676, Wl_2/M 7·725, A/Wl_2 1·500, A/M 11·54.

24

Fig. 24.—*Protoneura tenuis* ♀, Brazil: State of Pará, Belem, 7.viii.1922 (*J. H. Williamson & J. W. Strohm*), teeth on outer valve of ovipositor, left lateral view.

Material Examined. Peru: Iquitos, Dept. Loreto, May 1938, 1 ♂ (holotype); April 1936, 1 ♀ (allotype) (*G. G. Klug*). The types will be deposited in the British Museum (Natural History).

Protoneura klugi is a member of a closely related group of species, the *tenuis* group, and within that group it appears to be most nearly related to *scintilla* Gloyd, 1939; though not closely related to *woytkowskii* Gloyd, 1939, it approaches this species rather than *tenuis* in the following characters: pale antealar sinus of male and female, mid-dorsal thoracic stripe of male, colour-pattern of abdominal segment 9 of male, abdominal appendages of male, coloration of frons and broad antehumeral stripe of female; on the other hand the penis might be considered as an exaggerated form of that of *calverti* Williamson, 1915, or of *macintyrei* Kennedy, 1939. From *scintilla* and the other species of the group it is distinguished by a combination of characters, the black tibiae, the colour-pattern of the head, thorax and abdominal segment 9, and in the male by the structure of the penis and abdominal appen-

[9] In *P. tenuis* 1 ♀ the teeth are much shorter and narrower, 19–20 in number, and preceded by 2 even smaller ones (fig. 24).

[10] The definitions of these measurements are given below, p. 158.

[11] A discussion of these ratios is given below, p. 161.

dages. These distinctive characters are dealt with more fully in the key on p. 171. Mrs. Gloyd's notes (1.iii.38) on the female read : " The color pattern is very similar to that of *scintilla* ♀. Differs on head by having median spots of frons joined to pale area of genae; no pale lateral triangle on eye margin. Prothorax about same. Thorax : pale stripe on middorsal carina shorter. Metepimeral black stripe not connected basally with ventral black. Abd. : coloration about the same. Lower half of valve of ovipositor black, lower margin with fewer and longer teeth. Mesostigmal lamina not same as *scintilla* or *calverti* but more nearly like *tenuis*. I believe the thoracic and leg coloration would prevent it being *woytkowskii*.[12] Compared with *tenuis*, *calverti*, *scintilla* and is not same as any of them."

Definitions of Measurements.

In the description of this new species I have introduced a number of new measurements, the general practice up till now having been to give only the length of the abdomen and of the hind-wings, and in some cases also the width of the hind-wing and the length of the pterostigma. It has seemed to me that the use of the abdominal length as a standard measurement is subject to the disadvantage that, combining as it does the separate lengths of ten segments, it may be considerably variable, and that at least the head, thorax and legs, as the other major portions of the body, should be taken into account. I have therefore tried to find the easiest and most suitable measurements to take in order to give a fairly adequate summary of the sizes of the body-parts; I appreciate that only when such new measurements have been applied to diverse groups of related species can it be determined which are of value taxonomically and which, though ideally still a part of a " complete " description, are unnecessary in the present state of our Odonate studies. It must be borne in mind that even the universally accepted abdominal length, for example, gives taxonomic distinctions in only some groups of related species, and not in others; one cannot expect any newly proposed measurement to give taxonomic results in every case to which it is applied. The additional time required in making these measurements is shorter than one would think, if they are made systematically, and the labour will be well worth while even if only few of them prove in time to be useful taxonomically. For certain of these measurements I suggest conventional abbreviations, not to take the place of the verbal definitions, but to supplement them in avoiding constant repetition in discussion. As I am mainly concerned here with the Zygoptera, it may be necessary to modify or replace some of these standards when dealing with Anisoptera. A careful definition of the measurements is essential if the results of one author are to be strictly comparable with those of another.

It is difficult to make satisfactory measurements of the *head*, particularly of its length, owing to the different planes on which the parts of it lie, and the consequent variation to be expected from a slight shift in viewpoint might render the results unreliable. A visual comparison of the heads of *Coenagrion puella* (Linnaeus, 1758) and of *Epipleoneura ephippigera* (Selys, 1886) suggests that the head of the former is relatively very much longer and more robust, but this is certainly in some part illusory, as the following measurements will show (for comparison the measurements are calculated to an arbitrary scale) (table I).

[12] At this time Mrs. Gloyd had not yet seen females of *woytkowskii*; her belief has been fully realised.

TABLE I.

Relative dimensions of head to an arbitrary scale.

	C. puella ♂	*E. ephippigera* ♂
Maximum width between the eyes, dorsally (Ho) .	100	100
Maximum width, including the eyes, dorsally (He).	137·7	160·3
Minimum width, frontal view	62·32	61·44
Median length dorsally, from anterior border of postclypeus	54·61	50·60
Maximum length dorsally, from anterior border of postclypeus (Hl)	75·38	90·36

Taking the maximum dorsal length, *C. puella* has the head relatively shorter than *E. ephippigera*, and not, as one would expect from visual examination, relatively longer; this is no doubt due to the laterally more swollen occiput of *E. ephippigera*, but even taking the median dorsal length, *C. puella* has only a slightly relatively longer head. Considering these two species as examples of what appear to be robust and delicate-headed forms respectively, I would suggest the following standard head measurements, of those in table I the one made constant and the two which then show the greatest variation (in the Anisoptera at least the standards would no doubt be different): Maximum width of the occiput (Ho) between the inner margins of the eyes, measured in dorsal view with the vertex (ocelli) on a horizontal plane; maximum width of head and eyes (He), measured between the outer margins of the eyes in dorsal view with the vertex (ocelli) on a horizontal plane; maximum length of head (Hl), measured parallel to the median line of the head from the anterior margin of the postclypeus to the most caudal point of the posterior margin of the head, these two points being oriented on a horizontal plane.

Although the *prothorax* ought logically to be included in any system of measurements, I have not attempted it here, as it is relatively small, rather complicated in structure and often obscured. For the *pterothorax* I suggest the length of the mesepisternum (M) measured in dorso-lateral view from the postero-ventral angle of the mesostigmal lamina to the external angle of the antealar sinus with these two points on a horizontal plane; width of pterothorax (P) measured more or less in lateral view from the most dorsal point of the median crest of the antealar sinus to the posterior angle of the latero-ventral carina with these two points on a horizontal plane.

The *legs* could provide a very extensive set of measurements of three femora, tibiae and tarsal segments, but as will be seen from the discussion of ratios below (p. 161), in the Zygoptera the tibiae are generally but little longer than the femora, the range of the ratio being fairly small, and the greatest difference is between the first and third tibiae. I therefore measure the greatest length of the first and third tibiae (T_1, T_3) from the base to the apex, but not including any apical spines where these occur. (The number of femoral and tibial spines and their length relative to the distance between them have been dealt with above, p. 148, footnotes 2, 3.)

Wings: the length of the hind-wing is already accepted as a standard measurement; as in some groups the two pairs of wings differ, sometimes considerably, in length and width, I propose as standards: the length of front and hind-wings (Wl_1, Wl_2) from the base in a straight line to the most

distal point of the apical margin; the maximum width (Wb_1, Wb_2) measured perpendicular to the costa. Similarly the pterostigma of both pairs of wings, the length in a straight line from the costo-basal to the costo-apical angle, including the bounding veins; the maximum width perpendicular to the costa, including the bounding veins.

The length of the *abdomen* (A) is measured from the base of segment 1 to the apex of the abdominal appendages, or to the most caudal point of the appendages; the length of the superior appendages in dorsal view (♂) or lateral view (♀) in a straight line from the apical margin of segment 10 at the mid-point of the base of the appendage to the most caudal point (if the appendages are curved ventrad, it would be better to make the measurement in lateral view); the length of the inferior appendages in lateral view in a straight line from the apical margin of segment 10 at the mid-point of the base of the appendage to the most caudal point; the length of the ovipositor in lateral view from the mid-ventral apex of sternite 8 in a straight line parallel to the longitudinal axis of the apical abdominal segments to the most apical point of the ovipositor, excluding the terminal style.

Table II.

Ratios of lengths of femora and tibiae.

	T_1/F_1	T_2/F_2	T_3/F_3	F_2/F_1	F_3/F_1	T_2/T_1	T_3/T_1
Onychogomphus forcipatus L. ♂	0·924	0·817	0·685	1·039	1·646	0·918	1·219
Cordulegaster boltonii Don. ♂	1·179	0·958	0·938	1·162	1·317	0·945	1·048
Aeshna cyanea Müll. ♂	1·163	1·043	0·990	1·256	1·613	1·127	1·373
Cordulia aenea L. ♂	1·060	1·019	1·108	1·312	1·663	1·262	1·739
Libellula quadrimaculata L. ♂	1·134	1·138	1·117	1·134	1·523	1·138	1·500
Nannophya pygmaea Ramb. ♂	1·040	1·000	1·075	1·158	1·579	1·114	1·633
Anisoptera, range	0·924–1·179	0·817–1·138	0·685–1·117	1·039–1·312	1·317–1·663	0·918–1·262	1·048–1·739
Range per cent.	24·25	32·84	47·95	24·32	24·32	31·56	49·59
Agrion splendens Harr. ♂	1·340	1·190	1·154	1·328	1·607	1·176	1·383
Rhinocypha quadrimaculata Selys. ♂	1·307	1·144	1·093	1·268	1·555	1·110	1·300
Lestes sponsa Hans. ♂	1·128	1·049	1·057	1·473	1·909	1·371	1·790
Megaloprepus caeruleatus Dru. ♂	1·436	1·210	1·170	1·319	1·564	1·111	1·274
Platycnemis pennipes Pall. ♂	1·310	1·184	1·149	1·310	1·681	1·184	1·474
Coenagrion puella L. ♂	1·322	1·078	1·013	1·422	1·767	1·160	1·353
Protosticta gravelyi Laidl. ♂	1·318	1·218	1·188	1·250	1·568	1·155	1·414
Epipleoneura ephippigera Selys. ♂	1·380	1·207	1·077	1·260	1·560	1·102	1·218
Protoneura klugi sp. n. ♂	1·282	1·048	1·019	1·313	1·531	1·073	1·220
Protoneura tenuis Selys. ♂	1·231	1·059	1·010	1·308	1·523	1·125	1·250
Protoneura woytkowskii Gloyd. ♂	1·229	1·043	1·009	1·314	1·557	1·116	1·279
Zygoptera, range	1·128–1·436	1·043–1·218	1·009–1·188	1·250–1·473	1·523–1·909	1·073–1·371	1·218–1·790
Range per cent.	24·00	15·47	16·29	16·38	22·50	24·39	38·04

Discussion of Ratios.

It is probable that the ratios between these measurements will prove to be more frequently of taxonomic significance than the measurements themselves. I suggest the use of the ratios between the standards (length and width) of each part of the body, and the ratios between each standard and a single basic one, for which I have adopted the length of the mesepisternum (M) as being easy to measure accurately and possibly less subject to variation than the length of the wings or, at the least, of the abdomen. These ratios should of course be supplemented by others which are known to be, or are likely to be, of value in various restricted groups. The basic ratios would then be as follows: He/Ho, Hl/Ho, Ho/M, Hl/M, P/M, T_3/M, Wb_2/Wl_2, Wl_2/M, A/Wl_2, A/M. T_1/M has been omitted as probably it is simply related to T_3/M; Wl_1/Wl_2 and Wb_1/Wl_1 may be added for groups in which the front wings differ from the hind-wings; the ratio of length to width of the pterostigma may also prove to be of value in certain groups; A/Wl_2 has been included as it has already been used to a certain extent. In determining what measurements and ratios to use for the legs, I calculated from the lengths of femora and tibiae the ratios T_1/F_1 (length first tibia/length first femur), T_2/F_2, T_3/F_3, F_2/F_1, F_3/F_1, T_2/T_1 and T_3/T_1 for a series of species of several families, with the results given in table II. Notice that for *Onychogomphus forcipatus* the ratio of tibia to femur, especially T_3/F_3, is much lower than in the other species, while in *Lestes sponsa* the interfemoral and intertibial ratios are higher. For the present group of *Protoneura* I have only used the lengths of the first and

Table III.

Measurements in mm.	*Coenagrion puella* ♂	*Epipleoneura ephippigera* ♂	*Protoneura klugi* ♂	*P. klugi* ♀	*P. tenuis* ♂	*P. tenuis* ♀	*P. woytkowskii a* ♂	*P. woytkowskii b* ♂
He . .	4·16	3·09	2·95	2·84	2·93	2·88	3·14	3·14
Ho . .	3·02	1·93	2·05	1·98	2·02	2·07	2·00	2·09
Hl . .	2·28	1·74	1·35	1·42	1·42	1·40	1·44	1·46
M . .	3·11	2·91	2·38	2·33	2·40	2·28	2·52	2·56
P . .	2·98	1·91	1·91	1·88	1·86	1·81	1·98	2·00
T_1 . .	2·77	1·60	1·91	1·95	1·86	1·95	2·00	2·09
T_3 . .	3·74	1·95	2·33	2·38	2·33	2·38	2·56	2·61
Wb_1 .	4·00	3·91	2·47	2·77	2·47	2·47	2·98	2·98
Wb_2 .	3·93	3·63	2·45	2·72	2·42	2·42	2·95	2·86
O . .	—	—	—	1·53	—	1·46	—	—
Ratios								
He/Ho .	1·377	1·603	1·443	1·435	1·448	1·393	1·570	1·500
Hl/Ho .	0·754	0·904	0·659	0·718	0·701	0·674	0·721	0·700
Ho/M .	0·970	0·664	0·863	0·850	0·845	0·908	0·796	0·818
Hl/M .	0·731	0·600	0·569	0·610	0·592	0·612	0·574	0·573
P/M .	0·955	0·656	0·804	0·810	0·777	0·796	0·787	0·782
T_3/T_1 .	1·353	1·218	1·220	1·215	1·250	1·215	1·279	1·245
T_3/M .	1·202	0·672	0·980	1·020	0·971	1·041	1·019	1·019
Wl_1/Wl_2 .	1·048	1·050	1·086	1·056	1·057	1·086	1·054	1·081
Wb_1/Wl_1.	0·182	0·186	0·130	0·146	0·134	0·130	0·153	0·149
Wb_2/Wl_2.	0·187	0·182	0·140	0·151	0·138	0·138	0·159	0·155
Wl_2/M .	6·751	6·871	7·351	7·725	7·291	7·675	7·341	7·228
A/Wl_2 .	1·381	1·650	1·857	1·500	1·886	1·514	1·865	1·946
A/M .	9·324	11·34	13·66	11·54	13·75	11·62	13·69	14·07

third tibiae, and their ratio, as it is this latter which shows in both suborders the greatest range of variation.[13]

The measurements and ratios for the species of the *tenuis* group which I have been able to examine are summarised in table III, with the addition of data for *Epipleoneura ephippigera* ♂ and *Coenagrion puella* ♂ for comparison. The specimens studied are:—*P. klugi* ♂ holotype, ♀ allotype; *P. tenuis* 1 ♂, 1 ♀, Brazil: Belem, State of Pará, 7.viii.1922 (*J. H. Williamson & J. W. Strohm*); *P. woytkowskii* 2 ♂ paratypes—*a*, Peru: Rioja (*Dr. P. Martin*),[14] *b*, Bolivia: Buena Vista, Depto. Santa Cruz, ii.1933 (*F. Steinbach*). Additional data from the descriptions for the ratio A/Wl_2 are given in table IV.

Table IV.

	A/Wl_2	Mean [15]
P. macintyrei ♂ holotype	1·667	1·667
♀ paratype	1·375	
♀ allotype	1·450	1·436
♀ paratype	1·484	
P. tenuis ♂ holotype	1·777	1·832
♂ [16]	1·886	
♀ allotype	1·472	1·493
♀ [16]	1·514	
P. klugi ♂ holotype [16]	1·857	1·857
♀ allotype [16]	1·500	1·500
P. woytkowskii a ♂ holotype	1·848	
a ♂ paratype [16]	1·865	1·886
b ♂ paratype [16]	1·946	
a ♀ allotype	1·509	1·509
P. calverti ♂ [17]	—	(1·888)
♀ [17]	—	(1·547)
P. scintilla ♂ holotype	1·983	1·983
♀ allotype	1·618	1·618

Corrections and Additions to Previous Descriptions.

The following small errors have been detected in the descriptions hitherto published, and I have added some further notes on the few specimens studied by me, and listed above.

P. calverti.—In Cowley and Gloyd (1938 : 17, 5th line from bottom) metinfraepisternum should perhaps be *mesinfraepisternum*, as the character there

[13] This "range of variation" I have expressed as a percentage of the mean of the two extreme values of each ratio; it is perhaps not of much statistical value, but the calculation of the coefficient of variation (V) from a heterogeneous series of single specimens would seem also to have but little statistical value.

[14] The envelope containing this specimen bears a note by Mrs. Gloyd: "Color pattern darkest of the 9 paratype ♂'s"; but evidently subsequently at least one darker male was found in the paratype material from Ecuador, since it is one of these which is figured as the darkest (Gloyd, 1939 : fig. 3).

[15] The mean ("average") lengths of abdomen and hind-wing given in the descriptions cannot properly be used here, since the ratio of two means of measurements is not equivalent to the mean of the ratios of the measurements, except in special cases.

[16] The specimens studied as detailed above, p. 161.

[17] The range and average of the lengths of abdomen and hind-wing only being available in the description, the "average" ratio has of necessity been calculated from the means of the measurements of 7 ♂, 4 ♀; see footnote 15 above.

given seems to apply to this more markedly than to the metinfraepisternum, judging from pl. V fig. 1.

P. macintyrei.—In Kennedy (1939 : 6) the lengths of the abdomens of the paratype females have been given as the lengths of the hind-wings, and *vice versa.*

P. scintilla.—The description of the abdominal appendages of the male in Gloyd (1939) states : superiors slightly longer than inferiors (p. 3); superiors 0·3, inferiors 0·4–0·5 mm., inferiors extend 0·05–0·08 mm. beyond the apex of superiors (p. 7); superiors extending slightly beyond inferiors (p. 8, and pl. II figs. 2, 3). Evidently the statement on p. 3 should be emended so as to make it clear whether length or extension is meant, and the latter statement on p. 7 should be corrected by substituting *superior* for *inferior*, and *vice versa.*

P. tenuis.—In Cowley and Gloyd (1938) the last heading to table I on p. 10 should be *metepisternal* pale stripe, not mesepimeral.

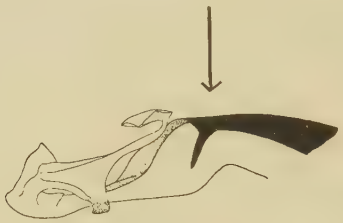
In the male studied there is just visible on the dorsal surface of the head a small obscure brownish triangle at the margin of the eyes on a level with the posterior ocelli; this triangle is not visible in the female. ♂ spines on femora, anterior series 3, 5, 5–6, posterior series 3–4, 5, 8–9, tibiae anterior series 3 + 7–9, 5, 7; on the femora distal anterior spine 0·80, 0·67–0·91, 1·10 times the length between its base and the base of the preceding spine, on the tibiae proximal anterior spine 0·80–0·86, 0·62, 0·68–0·82 times the length between its base and the base of the succeeding spine. ♀ femora anterior series 3, 5–6, 6, posterior series 4, 7, 7, tibiae anterior series 3 + 7–9, 5, 6; femora 0·73, 0·83, 0·91, tibiae 0·65–0·71, 0·67–0·68, 0·71. Median lobe of labium cleft to 0·52 (♂), 0·46 (♀) of its length. Apical carinae of abdominal segments 7–9 only distinctly denticulate.

P. woytkowskii.—The description in Gloyd (1939 : 9) states that abdominal segment 7 of the male has an anteapical ring separated mid-laterally from the narrow lateral margin; there is no pale *anteapical* ring on 7 in the two males before me, but the pale *basal* ring on 7, not mentioned in Gloyd (1939), is separated mid-laterally from the pale narrow lateral margin. I assume that *basal* should be read for anteapical.

♂ femora anterior series *a* 3, 4–6, 7, *b* 3, 5, 8, posterior series *a* 3, 6–8, 6–7, *b* 5, 9, 10, tibiae anterior series *a* 3 + 7, 5–6, 5, *b* 3 + 9–11, 8, 8; femora *a* 0·46–0·60, 0·44, 0·38–0·62, *b* 0·62–0·64, 0·54, 0·64–0·73, tibiae *a* 0·71–0·79, 0·40–0·50, 0·53, *b* 0·83, 0·85, 0·71–0·73. Median lobe of labium cleft to 0·48 of its length in both males. Apical carinae of abdominal segments 7–9 only distinctly denticulate.

The differences in colour-pattern between the males from Peru and Ecuador, and the single male from Bolivia, have already been described by Gloyd (1939); I refer to these two forms as *a* and *b* respectively, and the following notes are based on the examination of a single male of each form. The ventral laminar swelling of the superior appendages of *b* appears to be intermediate in shape between that of *woytkowskii a* (Gloyd 1939 : pl. II fig. 7) and that of *klugi* (fig. 12 of the present paper); compared with *a* the lamina is directed more caudad, the apex is more acutely rounded, the base is narrower, the upper margin straighter; also the apex approaches much more closely the down-turned apex of the appendage. I do not think that these differences are due to the position of the appendages, but they might be due to distortion of the lamina in drying. The penis of *b* (figs. 26–27) differs quite markedly from the Peruvian paratype figured by Gloyd (1939 : pl. II figs. 9–10) in

having a long apical strap-like process [18] to the third segment, which is absent in the Peruvian paratype figured by Gloyd; but in the penis of *a* from Peru studied by me (fig. 25) this apical strap is present although much shorter than in *b*, and it has been bent back on itself (no attempt was made to straighten out this delicate structure after the process of softening, for fear of damage and loss), its apex is symmetrically tapered and evidently not broken off. I believe therefore that the penis figured by Mrs. Gloyd is either abnormal or,



25

Fig. 25.—*Protoneura woytkowskii a* paratype ♂, Peru: Rioja (*Dr. P. Martin*), left lateral view of penis (the arrow indicates the approximate position of the apex of the third segment if this were unbent).

as is more likely, the delicate apical strap has been broken away. In both *a* and *b* the lateral dorsally directed lobes are sclerotised, particularly their dorsal margin, in lateral view the length from the ventral margin of the segment to the dorsal margin of the lobe is *a* 0·170, *b* 0·216 mm., the narrowest part of its stem *a* 0·049, *b* 0·071 mm. wide, ratio of this width to the distance from the base of the segment to the basal margin of the lobe *a* 0·277, *b* 0·515; length of median apical process from the level of the apical margin of the lateral lobe, *a* 0·422, *b* 0·552 mm., ratio of this length to the distance from the base of the segment to the apical margin of the lateral lobe, *a* 1·883, *b* 2·642.

26

27

Figs. 26–27.—*Protoneura woytkowskii b* paratype ♂, Bolivia: Depto. Santa Cruz, Buena Vista, ii.1933 (*F. Steinbach*), dorsal and left lateral views of penis.

On these and the colour characters I would consider *woytkowskii* to consist of two subspecies, one from N. Peru and Ecuador (*a*), the other from Bolivia (*b*); but I refrain from proposing a subspecific name for *b* in the absence of further data on the appendages and penis of *a* and of further specimens from Bolivia.

The *tenuis* Group of *Protoneura*.

Historical.

The first species of this group to be described, by Selys-Longchamps (1860), was *tenuis*; Williamson (1915) described *calverti*, but it was not until Cowley

[18] In fig. 27 this strap appears rather broader than it really is, as it is tilted somewhat laterad in the specimen.

and Gloyd (1938) redescribed *tenuis* and compared it with *calverti* that it was realised that the two species were closely related. Gloyd (1939) described two more species, *scintilla* and *woytkowskii*, and recognised that the four known species formed a nearly related group. Kennedy (1939) added a fifth species, *macintyrei*, and the present paper describes a sixth, *klugi*. All six species are known from both sexes, and have been carefully described and figured on a more or less common plan, so that although I have seen only three of the species, and but few specimens of these, I have no hesitation in offering the following discussion of their relationships and a key to the species, based principally on the literature. It is of course to be expected that the conclusions reached may be subject to some modification when there are more data on the distribution of the species at present known, and when any further species are added to the group. I do not believe that any of the other known species of the restricted genus *Protoneura* fall in this group, although the majority are known to me from descriptions alone. In what follows I have used the initial letters of the specific names instead of the full name, as a convenient abbreviation to avoid continued repetition: C = *calverti*, K = *klugi*, M = *macintyrei*, S = *scintilla*, T = *tenuis* and Wa, Wb = *woytkowskii* ***a*** and ***b***.

Relationships of the species.

Gloyd (1939 : 16) wrote : " In many species of Zygoptera the black pattern of the adult is only partially indicated in teneral specimens and gradually develops with age. If the evolutionary trend follows the same course and if relationships between closely related species can be traced through the medium of color patterns, then the one with the least extensive black areas may be considered the most primitive in this character." (I would like to emphasise that it is the *evolutionary trend* which is being discussed, and not a definite phylogeny.) It is generally considered that the females of Odonata are more primitive (less specialised) than the males in a large number of characters, and accepting the above hypothesis of the evolution of colour patterns one would expect to find that the females of these *Protoneura* species would be less extensively black than their males, and this one finds actually to be the case, *except* that the mesepisterna and abdominal segment 9 are *more* extensively black than in the males, which perhaps one may explain on the assumption that in the males these two areas have been specialised, by extension of the pale or non-extension of the black colour, as " recognition marks." Gloyd (1939) found that the four species known to her formed a series, proceeding from less to more black, as follows: WSTC; Kennedy (1939), without attempting to place *macintyrei* in this series, concluded that it was most nearly related to *woytkowskii*. If the six species be arranged in order of increasing black for each of the following 16 (♂) or 14 (♀) colour characters, anteclypeus, genae, frons, pale triangles on top of the head against the eyes, anterior, middle (♂) and posterior lobes of the prothorax, mid-dorsal pale stripe of pterothorax, pale antehumeral stripe, antealar sinus, first and second dark lateral stripes of pterothorax, venter of pterothorax, legs, abdominal segments 2 (♂) and 9, numbering the members of a series consecutively (1 being the least black member of a series, giving the mean value of their positions to such species as do not differ among themselves in a character, and giving the mean value of the whole series to any species for which the condition of the character is not known), and then for each species summing its numbers in all the series, finally rearranging the species in the order of these sums

gives: ♂ WbMWa/KSTC, ♀ WMKSTC, ♂ + ♀ WMKSTC (in the male series Wa stands much further apart numerically from K than K does from C). Taking another set of characters, and selecting that direction of each series which places M nearest the beginning, for (1) decreasing altitude of habitat,[19] (2) distribution from west to east,[20] (3) increasing length of abdomen, (4) increasing difference in length of abdomen of ♂ and ♀, (5) increasing ratio of lengths of abdomen to hind-wing, (6) increasing difference of this ratio between ♂ and ♀, (7) increasing ratio of width to length of hind-wing, (8) increasing ratio of He/Ho in ♂, (9) increasing ratio of Hl/Ho in ♂, (10) increasing ratio of Ho/M in ♂, the summation results in the series ♂ MWaTWb(CK)S, ♀ KTM(CW)S, ♂ + ♀ MTWKCS. Adding the total figures of each set gives: ♂ MW/S(KT)C, ♀ WMKTSC, ♂ + ♀ MWKTSC; or if the result of each set is given equal value and before adding together is renumbered consecutively from 1, this gives: ♂ M(WaWb)TKSC, ♀ KMWTSC, ♂ + ♀ MW(TK)SC. From the second set and the combined series from both sets it will be seen that, M having been selected to be near the beginning, C again falls at or near the end as in the first set. In the second set characters 3–6 may be considered as indicating increasing specialisation, but the precise evolutionary value of the remaining characters in this set is not at all clear. In a general way the second set bears out the result from the first, but because the second set is a heterogeneous assemblage of characters not united by a common hypothesis as is the first, it is best to place the chief emphasis on the first set of (colour) characters. The results of this first set for the two sexes separately and together are in almost entire agreement; on the other hand, in *macintyrei* the female is more similar to the male in colour characters and in length of abdomen and ratio of lengths of abdomen to hind-wing than are those of the other species, and for this reason I regard *macintyrei* as the most primitive member of the group; I therefore propose to place *macintyrei* at the beginning of the series, instead of as the second member separating the two possible subspecies of *woytkowskii*, so that the series has finally this order: MWbWa/KSTC. MW may be separated as a distinct subgroup; it is also noticeable that the remaining four species fall into two related pairs, KS and TC, but these two pairs have more characters in common than they have with the pair MW (in this pair also the dimensions of abdomen and hind-wing show greater variation than do those of the other species); the form of the superior abdominal appendages of the male (principally the ventral lamina) also is not inconsistent with the serial relations and grouping in pairs.

Reviewing the geographical distribution (fig. 28), one is tempted to suggest that the group originated in the west of the Amazonian region and from there spread eastwards and to lower altitudes; however, our knowledge of the distribution is still very incomplete, and in attempting to construct a phylogeny from our " evolutionary trend " series, it must be remembered that there is nothing, except our hypothesis as to colour development, to indicate what starting-point to take for a phylogenetic tree, whether a terminal or a middle

[19] Wa above 2000 ft., Wb below 2000 ft., C below 1000 ft., KST below 500 ft. The altitudinal distribution of M is not clear, as no localities are specified by Kennedy (1939), but only the Ecuadorian province of Los Rios. It is not clear whether the altitude given, 15 metres, is that of Guayaquil or of the collector's localities; it is certainly not that of Los Rios as a whole, for the province extends from a low altitude to the western slopes of the Andes.

[20] KSTW are from the Amazon drainage system, M from the Pacific coastal drainage system, C from the Essequibo drainage system and Trinidad. The west to east distribution (see fig. 28) gives MWaKSWbCT.

member of the series. Structural characters which run counter to the series are: ♂ inferior abdominal appendages shorter than superiors in MS, subequal in K, longer in CTW; apex of third segment of penis expanded laterally in CKMT, apex not expanded but the lateral margin expanded laterad at about mid-length in SW. But these two structural characters cannot be arranged in a simple linear evolutionary series, and the form of the penis at least is sufficiently varied to make it difficult to suggest relationships based on it.

28

Fig. 28.—Sketch-map of South America showing the distribution of the *Protoneura tenuis* group. C, *calverti*; K, *klugi*; M, *macintyrei*; S, *scintilla*; T, *tenuis*; Wa, Wb, *woytkowskii a, b.*

That this is a group of species and not a group of subspecies of one form is shown by the structural differences, particularly between the males, and the presence of at least a tendency to subspeciation in *woytkowskii*; in the absence of further material it is not possible to decide whether this is only a tendency or whether a distinct subspecies has been formed.

Discussion of the characters of the genus Protoneura *and of the* tenuis *group.*

Williamson (1915) used the following characters to restrict the genus *Protoneura*:—(1) wings narrow, width about $\frac{1}{7}$ the length or less; (2) first antenodal costal space longer than the third, and about twice or more the

second; (3) Rs (subnodal sector, IR_3) arising at the subnodus, M_3 (median sector, R_{4+5}) proximal; (4) M_2 (nodal sector, R_3) arising at or just proximal to the fifth postnodal in the front wings, at or just proximal to the fourth in the hind-wings; (5) M_3 (median sector, R_{4+5}) ending distal to the pterostigma. The species of the *tenuis* group agree with characters 2, 3 and 5, but some modification is necessary to characters 1 and 4. The width of the wings varies from about $\frac{1}{8}$ to slightly less than $\frac{1}{6}$, but as according to Williamson (1915) the other genera separated off from *Protoneura* have the width $\frac{1}{8}$ the length or more, the character does not, on our present knowledge, actually intergrade, though its taxonomic value is certainly somewhat reduced. The nodal sector arises front wings at the fourth to beyond the sixth, hind-wings beyond the third to beyond the fourth postnodal; but in the other genera Williamson (1915) used the origin of the nodal sector as a specific, rather than as a generic, character. Williamson (1915) then separated *calverti* and *corculum* Calvert (1907) from other species of *Protoneura* by character 6, and *calverti* from *corculum* by characters 7–9; (6) Cu_1 (superior sector of triangle, Cu_2) ending against or at the termination of, not crossing over, the cross-vein (subnodal transversal) descending from the subnodus; (7) wings extremely narrow, the width about $\frac{1}{8}$ (as against about $\frac{1}{7}$) the length; (8) base to nodus over $\frac{1}{3}$ (as against about $\frac{1}{3}$) the wing-length and equalling the distance from nodus to beyond the sixth (as against to beyond the fifth) postnodal; (9) first antenodal costal space nearly equalling the other two together (as against only slightly longer than the third). Character 6 fails as an absolute diagnostic feature of the *tenuis* group, as already pointed out by Cowley and Gloyd (1938 : 16) (only 75·6 per cent. of all the wings of *tenuis* would place it in the group by this character; for all six species I find only 70 per cent. of the wings possess this character), and the best one can do is to use the *tendency* of the character (omitting *klugi*, the data for which are based on only two specimens, the figures for this character suggest that it tends from the more variable condition in *woytkowskii* to apparent constancy in *calverti* in the order WTSC). Character 7 also fails completely, see the discussion above as character 1; for character 8 I have examined *tenuis* 4 ♂, 4 ♀ and *klugi* 4 ♂, 4 ♀ wings and find that in *tenuis* ♂♀ and *klugi* ♂ the distance base to nodus may fall just proximal to the 6th postnodal, in *klugi* ♀ just distal to the 5th, and in *klugi* ♀ front wings is a little less than $\frac{1}{3}$ the length of the wing, so that this character also fails completely, leaving only character 9 to distinguish the *tenuis* group absolutely from *corculum*; *corculum* is, however, easily distinguished from the *tenuis* group by, among other characters, the entirely different abdominal appendages of the male and mesostigmal lamina of the female.

With regard to characters 6 and 9, Williamson (1915 : 617) pointed out that in 6 *corculum* is like *calverti*, in 9 it is like *amatoria* and other species. He then continued: "If *calverti* and *amatoria* were separated generically the question of the generic position of *corculum* would be in doubt, and two decisions, in the absence of other determining factors, would be possible: One of the two characters could be regarded as the more important and *corculum* could be associated generically with one or the other species; or a new genus could be erected for *corculum*. That is to say, with our present knowledge, the existence of the species *corculum*, having one venational character of *calverti* and another venational character of *amatoria*, makes the generic separation of *calverti* and *amatoria* impractical. Were the number of species involved large, and were such possible new genera not monotypic, added

convenience might permit the erection of such new genera; at the present time there seems no warrant for such a minute breaking up of the genus." It is now known that *calverti* is only a member of a group of six species, and that in this group character 6 is variable, so that character 9 must be regarded as the more important; on Williamson's suggestions, therefore, a new genus could be erected for the six species of the *tenuis* group, based on character 9, restricting *Protoneura* to *corculum*, *amatoria* and other species. Nevertheless it seems premature to adopt such a course until its advisability has been demonstrated or refuted by more detailed study of other species of *Protoneura*; for the present, at least, *tenuis* and the five species related to it are best left as a group within the genus.

Taxonomic value of the postnodal and postsubnodal series of cross-veins.

From the combined data on 734 wings of *macintyrei*, *klugi*, *scintilla*, *tenuis* and *woytkowskii* it may be seen that in both wings the range in number of the postsubnodals is less than that of the postnodals; in both wings the frequency distribution of the postnodals is flatter and with a less well-defined mode, there being two numbers of postnodals almost equally frequent, while the distribution of the postsubnodal numbers is steeper and with a better defined mode, there being only one number of postsubnodals which is distinctly the most frequent, in both wings this being equal to the lower of the two more frequent postnodal numbers. On the other hand, the coefficients of variation (V) are very similar, being front wings postnodals 8·02, postsubnodals 7·52, hind-wings 7·19, 7·28. The smaller range and better defined mode of the postsubnodals in this group indicate that there is here a slight advantage in using the postsubnodal series instead of the postnodal series. Gloyd (1939 : 14), however, concluded from the combined data on 616 wings of *scintilla*, *tenuis* and *woytkowskii* that there was no significant taxonomic advantage in using postsubnodals instead of postnodals.

The revised definition of the genus *Protoneura* (*sens. str.*) follows, together with an attempt at the definition of the *tenuis* group of the genus, although in the absence of comparable studies of the other species of *Protoneura* it is difficult to decide what characters are diagnostic of the group, some which are included possibly being shared by other species or groups of species; nor is it easy to describe in words the facies these species have in common; to supplement the definition reference should be made to the figures in this paper and in the papers cited in the list of references.

Revised definition of Protoneura *Selys*, 1857.

Labium with elongate lobes; legs short, femora not compressed, tibial spines short; postnodals 7–13; inferior sector of triangle (1A) absent, the subquadrangle bounded posteriorly by the wing-margin and shorter than the distance from base of wing to the cubito-anal cross-vein (ac); cubito-anal cross-vein (ac) distal to the level of the first antenodal; superior sector of triangle (Cu_2) ending at or less than one cell beyond the subnodal transversal; wings narrow, width less than one-sixth the length; first antenodal costal space longer than the third, and about twice or more the second; subnodal sector (IR_3) arising at the subnodus, median sector (R_{4+5}) proximal to it; nodal sector (R_3) arising from at the fourth to distal to the sixth postnodal in the front wings, from distal to the third to distal to the fourth in the hind-wings; median sector (R_{4+5}) ending distal to, or at least at the level of the distal end of, the pterostigma.

Definition of tenuis *group.*

(Definition based on *calverti* 16 ♂, 9 ♀, *klugi* 2 ♂, 2 ♀, *macintyrei* 20 ♂, 6 ♀, *scintilla* 26 ♂, 10 ♀, *tenuis* 88 ♂, 44 ♀, *woytkowskii* 130 ♂, 14 ♀ front wings and hind-wings, in all 282 ♂, 85 ♀ (367 ♂ + ♀) front wings and hind-wings, and on descriptions of half these numbers of specimens, except *calverti* 16 ♂, 6 ♀ specimens. The following signs indicate that data are not available for: * *calverti*; † *calverti* and *macintyrei*; § *macintyrei*, *scintilla* and *woytkowskii*; ‡ *macintyrei*.)

Black or dark brown with the following areas pale (cream or yellow unless otherwise mentioned): frons with a spot beneath each antenna and usually a pair of median spots (yellow or orange in ♂), which may be confluent with each other, with the subantennal spots or with the pale colour of the genae; prothorax with a pair of dorsal stripes at least on the middle lobe, in the ♂ very large and red or orange; mesepisterna with an antehumeral stripe, in ♂ broader and red, scarlet or orange, often with a narrow mid-dorsal stripe, in ♂ red, scarlet or orange; pterothorax laterally with a stripe on the metepisternum and metepimeron, in ♂ yellow, orange or bluish; pale colour of antealar sinus when present in ♂ red, scarlet or orange; venter of pterothorax largely or entirely pale; femora pale basally, dark apically; first antenodal costal space § nearly equalling the second and third together; postnodals front wing * 8 (0·3 per cent.), 9 (14·1), 10 (39·6), 11 (39·3), 12 (6·2), 13 (0·6), hind-wing * 7 (2·7), 8 (48·7), 9 (44·8), 10 (3·5), 11 (0·3); postsubnodals front wing † 8 (0·3), 9 (29·6), 10 (45·7), 11 (24·1), 12 (0·3), hind-wing † 7 (11·2), 8 (65·2), 9 (23·0), 10 (0·6); nodal sector (R_3) arising front wings ‡ from at the fourth to beyond the sixth postnodal (at the fifth in 93·1 per cent.), hind-wings ‡ from beyond the third to beyond the fourth postnodal (at the fourth in 98·4 per cent.); postnodal sector (IR_2) arising front wings § at or nearest the eighth (17·6 per cent.), ninth (71·7), tenth (10·7) postnodal, hind-wings § at or nearest the seventh (13·1), eighth (81·0), ninth (5·9) postnodal; superior sector of triangle (Cu_2) ‡ crosses the subnodal transversal (30·0 per cent.), ends against or at the termination of the subnodal transversal (70·0 per cent.); ventral margins of abdominal segments 1–9 pale to a varying extent, in ♂ on 1–2 yellow or pale blue, 3–6, 7 or 8 with a narrow basal ring which may be divided mid-dorsally to form a pair of basal spots, usually confluent laterally with the marginal ventral colour on the more anterior segments, in ♂ yellow, orange or blue, in ♀ yellow or blue, pale colour of dorsum of 2 when present orange, 9 with the ventral margin pale to a varying extent, sometimes extending more or less dorsally and in ♂ when meeting mid-dorsally or almost so orange or yellow; 10 in ♂ sometimes with one or two dorso-lateral spots orange or yellow; posterior margin of posterior lobe of prothorax simple, regularly curved, similar in both sexes; ♀ mesostigmal lamina simple, triangular; penis variable in form, the apex of the third segment either expanded as a lateral process, or the lateral margin expanded laterally at about mid-length; ♂ superior abdominal appendages subequal in length to segment 10, more or less tapered apically, the apex turned mesad and ventrad, more or less minutely hooked, ventrally with a laminar swelling of variable form placed more or less subbasally or at mid-length of the appendage, directed ventrad or ventrad and caudad; inferior appendages from two-thirds the length of to a little longer than the superiors, broad at base, then narrowed and more or less subcylindrical, simple. Length of abdomen plus appendages ♂ 29–37·5, ♀ 26·5–32, of hind-wing ♂ 15·5–21, ♀ 17–21·5, of ♂ superior appendage ‡ 0·3–0·52, of ♂ inferior appendage ‡ 0·4–0·9 mm.

P. woytkowskii subgroup: ♂ anterior lobe of prothorax with only the mesal two-quarters or less black, posterior lobe with only the mesal third or less black; pale antehumeral stripe in ♂ half the width and from three-quarters to all the length of the mesepisternum, not markedly longer mesally than laterally, in ♀ one-third the width and from three-quarters to all the length of the mesepisternum; ♂♀ metepisternal pale stripe reaches

the apical carina broadly; ♂♀ venter of pterothorax entirely pale; ♂♀ anterodorsal and ventral surfaces of first femora with the basal two-thirds pale; ♂♀ tibiae pale with a subbasal dusky band and the apical third or less dark; ♂ abdominal segment 2 often pale dorsally, 9 with a pale subapical ring (or very nearly a ring) on one-third or more of the dorsum.

P. tenuis subgroup : ♂ anterior lobe of prothorax black or almost entirely so, posterior lobe black; ♂ pale antehumeral stripe either almost as wide as the mesepisternum basally, in contact with the basal quarter to two-thirds of the mesopleural (humeral) suture mesally from about half to all the length of the mesepisternum, or from two-thirds to one-third as wide as the mesepisternum, in contact with the basal half to two-thirds of the mesopleural (humeral) suture, markedly longer mesally, to two-thirds of the mesepisternum, than laterally; ♂♀ metepisternal pale stripe not reaching the apical carina, or only narrowly; ♂♀ venter of pterothorax with dark markings behind the third coxae; first femora, anterodorsal surface almost all dark in ♂, at most only about the basal tenth pale, ventral (♂♀) and anterodorsal (♀) surfaces with the basal half or less pale; ♂♀ tibiae entirely dark brown or black; ♂ abdominal segment 2 not pale dorsally, on 9 the pale lateral or ventral colour does not meet mid-dorsally to form a complete ring.

Key to the species of the tenuis *group of* Protoneura.

1 (6). Venter of pterothorax entirely pale; tibiae pale with a subbasal dusky band and the apical $\frac{1}{3}$ or less dark; ♂ posterior lobe of prothorax with only the mesal $\frac{1}{3}$ or less black . . . *woytkowskii* subgroup. 2.

2 (3). Anterior lobe of prothorax with the mesal two-quarters, posterior lobe with the mesal third (♂) or two-quarters (♀), black; mid-dorsal pale stripe of mesepisterna absent; ♀ antehumeral pale stripe the whole length of mesepisternum; ♀ metinfraepisternum entirely pale; abdominal segment 9 in ♂ pale except for a narrow apical ring, in ♀ the lateral pale spot almost reaches the mid-dorsum; ♂ inferior abdominal appendages shorter than superiors; third segment of penis with the apex expanded laterally . *macintyrei* Kennedy, 1939.

3 (2). Anterior and posterior lobes of prothorax ♂♀ almost entirely pale; mid-dorsal pale stripe of mesepisterna present, on the apical half to almost all the length of mesepisternum; ♀ antehumeral pale stripe only on basal $\frac{3}{4}$ of mesepisternum; ♀ metinfraepisternum with some black; abdominal segment 9 in ♂ with the pale subapical ring dorsally equal to or less than the basal black, in ♀ the lateral pale spot only extends to about mid-height; ♂ inferior abdominal appendages longer than superiors; third segment of penis with the margin at about mid-length expanded as a lateral process, the apex of the segment produced mesally as a long strap-like process directed cephalad . . . . . *woytkowskii* Gloyd, 1939. 4.

4 (5). ♂ mid-dorsal pale stripe of mesepisterna almost as long as the sclerite; ♂ black stripe of mesepimeron occupying slightly more than the basal half of the sclerite, broadly separated from the apical carina by pale colour; ♂ metinfraepisternum entirely pale; ♂ dark stripe on metapleural (second lateral) suture very narrow, separated into an apical upper spot and a lower short stripe; ♂ abdominal segment 1 entirely yellow, 2 with no dorsolateral black bar, on 9 the pale subapical ring dorsally equal to the basal black; third segment of penis with the mesal apical process about $2\frac{1}{2}$ the length from the base of the segment to the apical margin of the lateral process, the narrowest part of the stem of the lateral process about half the length from the base of the segment to the basal margin of the lateral process. ♀ unknown . . . . . *woytkowskii b.*

5 (4). ♂ mid-dorsal pale stripe of mesepisterna on the apical $\frac{1}{2}$–$\frac{2}{3}$ of the sclerite; ♂ black stripe of mesepimeron only narrowly separated by pale colour from, or narrowly reaching, the apical carina; ♂ metinfraepisternum about half black; ♂ dark stripe on the metapleural (second lateral) suture broader, the apical upper spot and the lower stripe broadly confluent; ♂ abdominal segment 1 black or brown dorsally, 2 with a dorsolateral black bar confluent or not with the subapical transverse black bar, ♀ 9 the pale subapical ring dorsally equal to $\frac{1}{3}$ or less of the basal black; third segment of penis with the mesal apical process less than twice the length from the base of the segment to the apical margin of the lateral process, the narrowest part of the stem of the lateral process about $\frac{1}{4}$ the length from the base of the segment to the basal margin of the lateral process . . . . . *woytkowskii a.*

6 (1). Venter of pterothorax with dark markings behind the third coxae; tibiae entirely dark brown or black; ♂ posterior lobe of prothorax entirely black . . . . . *tenuis* subgroup. 7.

7(10). ♀ anterior lobe of prothorax largely pale with three more or less confluent rounded basal spots; ♂ mid-dorsal pale mesepisternal stripe present on the apical $\frac{7}{10}$–$\frac{4}{5}$ of the sclerite; antehumeral pale stripe in ♂ $\frac{1}{3}$–$\frac{2}{3}$ the width of the mesepisternum, in contact with the basal $\frac{1}{2}$–$\frac{2}{3}$ of the mesopleural (humeral) suture, longer mesally, to $\frac{2}{3}$ the length of the mesepisternum, in ♀ broader than the mid-dorsal pale stripe, $\frac{1}{5}$–$\frac{1}{4}$ the width and $\frac{1}{2}$–$\frac{2}{3}$ the length of the mesepisternum and widely separated from a small pale apical posthumeral spot; ♂ superior abdominal appendages slightly less than the length of segment 10 . . . . . 8.

8 (9). ♀ pale colour of genae confluent with mid-frontal spots; ♀ posterior lobe of prothorax with the mesal two-quarters black; ♀ mid-dorsal pale stripe of mesepisterna on the apical $\frac{2}{3}$ of the sclerite; antealar sinus in ♂ largely pale, in ♀ pale with a black latero-apical finger; antehumeral pale stripe in ♂ $\frac{1}{3}$ as wide as the mesepisternum, in ♀ $\frac{1}{2}$ the length of the mesepisternum; ♂ metepisternal pale stripe reaches the mesinfraepisternum; dark areas of venter less extensive; ♂ abdominal segment 9 with a large pale latero-ventral spot extending dorsad and almost meeting mid-dorsally; ♂ inferior abdominal appendages subequal to the superiors; third segment of penis with apical lateral processes . . . . . *klugi* sp. n.

9 (8). ♀ pale colour of genae not confluent with mid-frontal spots; ♀ posterior lobe of prothorax almost entirely pale; ♀ mid-dorsal pale stripe of mesepisterna on the apical $\frac{5}{9}$ of the sclerite; antealar sinus in ♂♀ almost entirely black; antehumeral pale stripe in ♂ $\frac{2}{3}$ as wide as the mesepisternum, in ♀ $\frac{2}{3}$ the length of mesepisternum; ♂ metepisternal pale stripe not reaching the mesinfraepisternum; dark areas of venter more extensive; ♂ abdominal segment 9 only narrowly pale ventrally; ♂ inferior abdominal appendages shorter than superiors; third segment of penis with small lateral lobes at mid-length *scintilla* Gloyd, 1939.

10 (7). ♀ anterior lobe of prothorax with mesal two-quarters black; ♂ mid-dorsal pale mesepisternal stripe absent; antehumeral pale stripe in ♂ almost as wide as the mesepisternum basally, laterally in contact with the basal $\frac{1}{4}$–$\frac{2}{3}$ of the mesopleural (humeral) suture, mesally less than half to nearly as long as the mesepisternum, in ♀ very narrow, not broader than the mid-dorsal pale stripe, $\frac{3}{4}$ the length of the mesepisternum, confluent or almost so with an apical posthumeral narrow stripe or series of small spots; ♂ superior abdominal appendages slightly greater than the length of segment 10. . . . . 11.

11(12). ♂ antehumeral pale stripe in contact with the basal $\frac{1}{3}$–$\frac{2}{3}$ of the mesopleural (humeral) suture, mesally half to as long as the mesepisternum, usually with an apical extension along the mesopleural (humeral) suture; ♂ metepisternal pale stripe reaches the mesinfraepisternum below, narrowly reaching or separated from the apical carina above; ♂ metepimeral black not confluent with the ventral black; ♀ metepisternal pale stripe reaches or almost reaches the apical carina above, broader basally, wider than the black stripe of the metapleural (second lateral) suture ventral to it; ♀ dark areas of venter less extensive; ♂ ventral lamina of superior abdominal appendages more prominent in lateral view; third segment of penis with apex expanded as broad lateral lobes; ♀ mesostigmal lamina with posterior margin not abruptly raised above the level of the thorax

tenuis Selys, 1860.

12(11). ♂ antehumeral pale stripe in contact with about the basal $\frac{1}{4}$ of the mesopleural (humeral) suture, mesally less than $\frac{1}{2}$ to $\frac{2}{3}$ as long as the mesepisternum, without any apical extension along the mesopleural (humeral) suture; ♂ metepisternal pale stripe broadly distant from the mesinfraepisternum below, and from the apical carina above; ♂ metepimeral black confluent with the ventral black; ♀ metepisternal pale stripe not reaching the apical carina above, narrower basally, not wider than the black stripe of the metapleural (second lateral) suture ventral to it; ♀ dark areas of venter more extensive and more sharply defined; ♂ ventral lamina of superior abdominal appendages less prominent in lateral view; third segment of penis with apical lateral lobes smaller; ♀ mesostigmal lamina with the posterior margin distinctly raised above the level of the thorax, giving it the appearance of an elevated ridge

calverti Williamson, 1915.

References.

Cowley, J., and Gloyd, L. K., 1938, Redescription of the types of *Protoneura tenuis* Selys and a study of variation in this species. *Occ. Pap. Mus. Zool. Univ. Mich.* **378**: 18 pp., 5 pls.

Gloyd, L. K., 1939, Two new species of *Protoneura* from South America (Odonata). *ibid.* **408**: 17 pp., 3 figs., 2 pls.

Kennedy, C. H., 1939, *Protoneura macintyrei*, a new species of dragonfly from Ecuador (Odonata: Protoneurinae). *ibid.* **410**: 8 pp., 2 pls.

Selys-Longchamps, E. de, 1860, Synopsis des Agrionines, dernière légion: Protonevra. *Bull. Acad. Belg.* (2) **10**: 431–462.

Williamson, E. B., 1915, Notes on neotropical dragonflies, or Odonata. *Proc. U.S. nat. Mus.* **48**: 601–638, 3 figs., pls. 38–44.